No. 4. — *Studies from the Newport Marine Zoölogical Laboratory. Communicated by* ALEXANDER AGASSIZ.

XVIII.

On the Development of the Calcareous Plates of Amphiura.

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IN a paper published in March, 1886,* it was shown that the egg of Ophiopholis develops into a pluteus-like larva in which the two lateral arms with calcareous rods are well developed. In the month of July of the past summer a similar larva was traced into an adult pluteus. This adult pluteus of Ophiopholis is the same as that doubtfully referred by A. Agassiz to *Amphiura squamata*, thus confirming the statements † made in the paper above quoted. While however it was possible to determine the general anatomy of the adult pluteus of Ophiopholis, circumstances rendered it impossible for me to follow the growth of the calcareous plates and skeleton in the body of the young Ophiopholis forming in this pluteus. It was more convenient to complete my studies of this part of the subject on another genus. For this work the well-known viviparous Ophiuran, *Amphiura squamata*, Sars, was chosen.

This species is well suited for the study. It is common near the Newport Marine Laboratory, and easily collected. It is viviparous, and the young are found in the parents through the months of August and September, when the Laboratory is open for work. Whatever disadvantages come from the possible retardation or acceleration in the sequence of the development of the plates brought about by the abbreviated development, is certainly offset by the ease with which material can be

* Preliminary Observations on the Development of Ophiopholis and Echinarachnius, *Bull. Mus. Comp. Zoöl.*, Vol. XII. No. 4, pp. 105–119. In this paper it was first shown that Ophiopholis has a nomadic pluteus.

† On p. 119 (*op. cit.*) it is said, "*Ophiopholis aculeata* has a development with metamorphosis, passing through a larval stage called the pluteus," and on p. 106, note, "The pluteus referred to *Amphiura squamata* in the 'Embryology of the Echinoderms,' and doubtfully to Amphiura in 'Embryological Monographs,' may be a pluteus of Ophiopholis." The embryology of *A. squamata* is partially traced in the following pages.

procured. My attention in the following observations was chiefly directed to the growth of the hard parts of the body, often called the skeleton, while observations on the bilateral larva are simply introduced as they are thought to throw light on some of the many obscure questions in relation to this part of the subject.

I. GENERAL OBSERVATIONS.

Many observers have called attention to the fact that *A. squamata* is viviparous. No one, so far as the literature has been studied, has seen the young in the American shallow-water Amphiura, although Lyman and others have shown its undoubted identity with the European, *A. squamata*. Of the other species of Amphiura which live in our waters no one has studied the development.

Metschnikoff * has shown that *A. squamata* is hermaphrodite. This observation has been verified by Apostolides,† and I have found the male genital glands in the Newport specimens in the same position as figured by Metschnikoff ‡ in the European. Almost every specimen of Amphiura which was collected in August and September was found to contain young, while some had the male glands with lively sperm and young in various stages of growth in the same individual. This fact may look like self-fertilization. It remains to be seen, however, whether the sperm from one individual can impregnate its own ova, or whether this product from another specimen is required for this function. I am not aware that any one has yet succeeded in artificially impregnating an Amphiura with its own sperm. Self-fertilization may take place, but no one has yet recorded it.

My specimens of the adults were found in crevices of the cliffs just below low-water mark. We found good collecting-grounds on the south end of Castle Hill, at Price's Neck, and near Horse's Head, Conanicut Island. The adults prefer a bottom composed of broken Mytilus shells and small stones. Lyman § has already spoken of their preference for a bottom of broken shells. With a long-handled dip-net a few handfuls of this bottom can be scraped up from the crevices, and the adults can be easily picked out of the fragments of shells with pincers.

* Studien über die Entwickelung der Echinodermen und Nemertinen, *Mém. de l'Acad. Imp. des Sci. de St. Pétersb.*, [7] XIV. 8, pp. 13, 14 (separate copy).

† 1e Thèse. Anatomie et Développement des Ophiures, *Arch. de Zool. Exp. et Gén.*, X. p. 204.

‡ *Op. cit.*, Pl. III. Fig. 1, B. Our *Amphiura squamata* is also hermaphrodite.

§ Ophiuridæ and Astrophytidæ, *Ill. Cat. Mus. Comp. Zoöl.*, No. 1.

The young were taken from the adult by cutting off the disk, leaving the arms intact. By removing the disk in this way it was found that the young remained in it, and when left for a short time in pure water the older specimens crawled into view. Lyman * has recorded that adults found near Bordeaux often in confinement voluntarily cast their disk, from which the orange-colored young emerge. The older forms of the young can voluntarily escape from the disk through the genital slits. Those which have an umbilical attachment, particularly the bilateral larvæ, must be teased from the ovarian attachment by means of needles or small scalpels when required for study. A delicate dissection is necessary to separate the larva from the inner wall of the body without harm to the attached young.

The larvæ were studied alive. Many were killed in weak alcohol, hardened in 93° alcohol, placed in chloroform for three minutes, and then mounted in Canada balsam. The treatment with chloroform brought out the plates with success. Staining in borax carmine showed the water-tubes, but obscured the plates.

Young Amphiuræ were found from the first of August until the end of September, with little reduction in numbers except in the last week. The number of young from different adults varied. Ordinarily a gravid adult would have from ten to fifteen (generally ten) free young, and possibly several bilateral larvæ at the same time. The older young live free in the body cavity, generally with the arms coiled up, but often with an arm extended through the genital slit. Parturition is moderately slow, sometimes rapid. The young when born are orange-colored on the disk, with whitish-colored arms, and with plates less firmly articulated than in the adult. When once born, young were not seen to return to the pouches, nor were they cared for by the adult. They did not cling to the mother after birth. Especial attention was directed to this observation, for I was familiar with the figures given by Thomson † of young Ophiurans of another genus clinging to the disk of the adult.

The young Amphiuræ which voluntarily left the parent were of course

* *Op. cit.*, p. 123.

† Notice of some Peculiarities in the Mode of Propagation of certain Echinoderms of the South Sea, *Journ. Linn. Soc.*, XIII. Dr. W. Stimpson (*Proc. Bost. Soc. Nat. Hist.*, IV. p. 226) found in Charleston, S. C., small Ophiurans clinging to the arms of *Hemipholis cordata*, Lym. (*Ophiolepis elongata*, Say). He regarded them as the young of the animal to which they were clinging, and thought that they "correspond" to the genus "Ophionyx, M. T."

Lyman (Challenger Ophiuroidea, p. 157) describes and figures two stages of the young Hemipholis which he finds clinging to the arms and disk, and "suspects" that the genus is viviparous.

in confinement in glass aquaria, which condition must be given its proper significance, and may have deterred them from clinging to the parents. In this connection let me mention an observation which has been repeatedly observed in dredging our common "basket-fish." The egg and early development of this animal (*Gorgonocephalus Agassizii*) is unknown, but the young with arms with a single bifurcation have repeatedly been brought up from the bottom clinging to the disk of an old adult. It is very necessary to find out whether or not the basket-fish is viviparous, as this would possibly indicate.

The young Amphiuræ are born at intervals, in a continuous series, not all at the same time. There are well-developed young of different sizes in the same parent. It was not possible to tell from the size, in all cases, whether the mother or adult had young in the body. Swollen specimens were ordinarily gravid, but many large specimens were without young.

When the disk of many swollen specimens was looked at from above (abactinal region), one or more of the interradial regions was observed to have a reddish color and to be more swollen than the remaining. On dissecting these specimens to learn the cause of the color and apparent abnormal condition, they were found to harbor in their bodies bundles of claret-colored ova. The development of these ova in the Amphiura was traced by opening several specimens. Eggs were found in all conditions of cleavage and larval growth, from very young specimens to an adult Crustacean (Copepod?). They are parasitic in nature, and pass their early life in the body of the Ophiuran. In several instances the ova of Amphiura were found with the ova of the parasite, but in most cases an amorphous reddish mass indicated the possible position of the ovarian gland of the host. The ova of the Ophiuran and those of the parasitic Crustacean can be readily distinguished by a difference in color which is well marked. The eggs of the Crustacean are found in bright red or pink clusters. Those of the Amphiura are red and orange, and not in free packets.

The ova of the Crustacean are unattached to the parent. They are often found without parent Crustacean. The development of the parasite will be treated in a special paper. None of the many attempts to produce artificially two Amphiurans by cutting the disk in halves led to positive success, although a six-armed Amphiuran cut in such a way that three arms were left in each half of the body lived as two individuals for a considerable time. They were not observed, however, to bud off new arms, as it was hoped they would do. Embryos with four and six arms were repeatedly found. Adults with six arms were common.

The disk in several instances was removed from its connection with the arms, and the five remaining connected arms lived for three days after the mutilation.

I had some difficulty in identifying the adult Amphiura, from the fact that in some of the best descriptions of *A. squamata* the color of the live animal is not given, while in others it is recorded as white.* None of the adults of *A. squamata* studied were white, but all were brown or chocolate colored when alive. Variation of color is great among specimens of the same genus, and in some localities this species may be white; but the specimens which were studied were not white.

II. THE BILATERALLY SYMMETRICAL LARVA.

August Krohn † and Max Schultze ‡ first found out that *Amphiura (Ophiolepis) squamata*, Sars, is viviparous; and that discovery has been established without possibility of doubt by Sars,§ Lyman,|| Metschnikoff,¶ Apostolides,** Ludwig,†† and others. Its viviparous life falls into the following divisions: (1) The development of the bilateral larva;

* Packard states (Zoölogy, p. 111): "*A. squamata*, Sars, has long slender arms and is white." In Agassiz's "Sea-Side Studies," p. 115, *A. squamata* is spoken of as the "white Amphiura."

The adults were identified by comparison with specimens in the Museum of Comp. Zoölogy identified by Mr. Lyman, and by reference to published descriptions. Prof. Verrill has also examined my specimens of the adults, and verifies my identification.

† Ueber die Entwickelung einer lebendig gebärenden Ophiure, *Arch. f. Anat. Physiol. u. Wiss. Med.*, 1851. Krohn first showed that *Amphiura* (*Ophiolepis*) *squamata* is viviparous.

The first naturalist to describe the young of *Amphiura* (*Ophiolepis*) *squamata* was Joh. Müller (*Arch. f. Anat. Physiol. u. Wiss. Med.*, 1851, p. 1 *et seq.*). He erroneously ascribed to Ophiolepis in this place a pluteus form. Following Krohn's paper (*op. cit.*, p. 353), where *Ophiolepis* (*Amphiura*) *squamata* is shown to be viviparous, it is acknowledged that the young described by Müller is of some other Ophiuran, and not *Ophiolepis squamata*.

‡ Ueber die Entwickelung von *Ophiolepis squamata*, einer lebendig gebärenden Ophiure, *Arch. f. Anat. Physiol. u. Wiss. Med.*, 1852.

§ Jahresbericht of Leuckart, 1865, p. 86.

|| Ophiuridæ and Astrophytidæ, *Ill. Cat. Mus. Comp. Zoöl.*, No. 1.

¶ *Op. cit.*, p. 13.

** *Op. cit.*

†† Zur Entwickelungsgeschichte des Ophiurenskelettes, *Zeit. f. Wiss. Zoöl.*, XXXVI.

and (2) The development of the pentagonal or stellate young, free in the body of the parent.

The youngest embryo of Amphiura which was observed by me is a blastosphere.

Blastosphere. — The blastosphere (Pl. II. Fig. 1) was found free in the body of a dissected adult, and had probably ruptured its connection with the parent. It closely resembles the blastosphere of some other Echinoderms, and is of about the same age as that of Amphiura figured by Metschnikoff* and by Apostolides.†

The few blastospheres of Amphiura which were found were unattached to the body walls or to each other. In later stages, as in the bisymmetrical larvæ, the young Amphiuræ are attached by a structure called the umbilicus. Sir W. Thompson has spoken of the free young of certain viviparous Echinoderms in the body cavity of adults, in his "Notice of Peculiarities in the Mode of Propagation of certain Echinoderms of the Southern Sea," ‡ as not appearing to have in any case an organic connection with the parent. It seems natural to suppose, if the bisymmetrical larva is attached, that the younger stages are not free; but I have no proof of this. It is supposed, not proven by observation, that the blastosphere is broken from its attachment.

The cells of the blastosphere are surrounded by two envelopes (m^1, m^2). I am unable to prove that either of these envelopes is "chitinartig," as Metschnikoff describes the apparently homologous outer envelope. The inner envelope resembles somewhat the cortical layer which I have described in the ovum of Ophiopholis where it is believed to be homologous to the *zona radiata* of other Echinoderms. Both envelopes are transparent. Diameter, .13 mm. The blastodermic cells are spherical, red in color. There is no ciliation on the outer surface of the blastodermic cells. Nucleus of each cell well seen. There is a segmentation cavity (*cav*) as in other Echinoderms.

Gastrula. — There is no free nomadic gastrula in Amphiura, but the blastosphere is followed by a larval condition (Pl. II. Fig. 3), in which we recognize certain characters of a gastrula. According to Metschnikoff,§ directly after the blastosphere stage there appears in the protoplasm of the blastodermic cells two layers of cells, "von denen die

* *Op. cit.*, Pl. III. Fig. 3. The "cavity" is lettered *v* (no explanation) in Pl. III. Fig. 5; *cs* in Fig. 4 (*cs*, Fig. 4, is the segmentation cavity).

† *Op. cit.*, Pl. XII. Fig. 9.

‡ *Journ. Linn. Soc.*, XII.

§ *Op. cit.*, p. 14.

untere körnig und roth die obere dagegen glassartig und homogen erscheint." A stage similar to his is figured in Pl. II. Fig. 3. The mode of formation of the cavity is not made evident in either Apostolides' or Metschnikoff's account. The inner layer of cells, or the red cells, is supposed to be the mesoblast; the outer, the epiblast; and the walls of the cavity, or hypoblast, are concealed by the mesoblast. It is possible that hypoblast and mesoblast have as yet not differentiated themselves in the red cells. The blastosphere unquestionably has a true segmentation cavity, but by the concentration of the pigmented cells near its interior, by which concentration the superficial layer (epiblast) of transparent cells appears to be separated, renders the interior of the egg so opaque that observation of the contents is almost impossible without cutting sections. As only one blastosphere and not more than four gastrulæ were found, my material was limited. The transparent outer layer (*ep*) is probably the epiblast, and the masses of reddish cells in the interior of the body of the embryo may be the same as the so-called amœboid or mesoblastic cells in other Echinoderm embryos. The true hypoblast either is not separated from the red cells or is differentiated from them and hidden by these opaque cells. There is what appears to be an external opening (*a*) passing into the opaque region of the ovum, which fact would seem to indicate the existence of a cavity. Unfortunately, however, I am not sure that such an opening exists. Apostolides, however, has described and figured this opening, and there is no reason to doubt its presence. It is necessary to have new observations on the existence of this primitive opening and the way it is formed. It disappears early in larval life. The mode of formation of the hypoblastic wall of the cavity of the gastrula of Amphiura has been interpreted in two ways. The first, and that which would seem the true one from what we know of other Echinoderms, is the embolic method; the second by delamination, unknown elsewhere in the group, is very exceptional and peculiar. Apostolides* supposes that in Amphiura the hypoblast is formed by a delamination of the blastodermic cells and not by invagination. Metschnikoff† says that it is formed by invagination. It is probable that the true blastopore was not observed by this naturalist, and the invagination which he observed was that of the mouth and possibly the œsophagus. This, however, does

* *Op. cit.*, pp. 25, 192.

† *Op. cit.*, p. 14, Pl. III. Fig. 6. A cavity with hypoblastic walls between it and the cutis (*c*) must have existed, as he speaks in the text of such a cavity ("Darmanlage"). His figures do not well represent the hypoblast.

not prevent our accepting the theory that the cavity of the gastrula is formed as Metschnikoff supposes.

In Ophiopholis it has already elsewhere been shown that the archenteron is formed by embole, and the known law of development in other Echinoderms would point to the same method in Amphiura. If there is an invagination of the blastoderm to form an archenteron in Amphiura, it is more masked than in Ophiopholis, and at present it is not possible for me to say whether Apostolides' or Metschnikoff's view of the mode of formation of the archenteron is the correct one. It looks very much as if the epiblast is separated from the reddish layer by a delamination, but it must be remembered that Amphiura is a viviparous genus, and possibly has a highly abbreviated * development in its early history. We may consequently suppose that more or less modification or concealment in the embolic mode in which the archenteron is generally formed in Echinoderms has resulted. It must also be remembered that the majority of gastrulæ of Echinoderms are embolic. My observations support in part Apostolides' statement that the primitive cavity, not however the segmentation cavity, of the gastrula is the intestine ("anus embryonnaire") of the future pluteus. Probably the stomach should have been included with the intestine. The external opening, if such exists, is early closed, and if it is lost, as it may be, from the attached life of the young Amphiura, is probably always functionless. We have the following statement in regard to the anus of the young Amphiura. Apostolides states: † "Dans le stade suivant, où l'ébauche du tube digestif est complètement dessinée, on distingue bien au sommet de l'estomac, au milieu d'un bourrelet, l'orifice anal." This would seem to show that there is an anal opening, but how it is formed cannot be answered so far as observation goes at present.

In his first paper Metschnikoff recognizes an opening into the cavity of the larva, and considered it as formed by an infolding of the blastoderm. He was probably mistaken in supposing this opening to be the primary opening, or blastopore. He is believed to have missed altogether

* The abbreviation in development which leads to the reduction in the arms of the pluteus stage in Amphiura is not believed to cause any great modification or variation in the development of the primary plates of the test and arms. One or two writers have brought to their aid, in speaking of the apparent discrepancy in the time of the development of these plates in Amphiura and an Ophiuran with a pluteus, the possibility of modification by abbreviation in the former genus. The argument is deceptive, and should not be given too great weight.

† *Op. cit.*, p. 208.

the blastopore, and the gastrula cavity or future intestine, as he confesses practically in a later paper.*

The following quotation from Apostolides leads me to suspect that this author did not clearly distinguish the mesoblastic cells in his young Amphiura with a single cavity (intestine) and single opening (anus). Possibly he confounded them with the hypoblast. He says:† "Dans l'ectoderme on commence à apercevoir quelques points orangés premiers indices de calcification." If these calcifications are really formed in the ectoderm or epiblast, it is exceptional among larval Echinoderms, where they are regularly formed in the mesoblastic cells. Metschnikoff ‡ rightly interprets the orange cells of the young Amphiura as mesoblastic or "cutis" cells. There is nothing in Apostolides' account either of Ophiothrix or of Amphiura to show that he recognized these cells which play such an important part in the growth of certain parts of the larval Echinoderm.

A study of Metschnikoff's Fig. 6. Pl. III.‡ is an instructive one. In this figure the epiblast (*ep*) is well formed, and the opening (an opening not figured, § but described in the text) on the lower pole is identified with the mouth opening of the older larvæ, which assume a bilaterally symmetrical contour. The young Amphiura is already bilaterally symmetrical, for on each side of the "opening" can be seen the beginning of the vaso-peritoneal vesicles, or water-tubes (*v*). At the pole opposite the supposed mouth there are trifid bodies (*cc*), identified as the provisional spines of the pluteus.

The homology of the parts of the larva mentioned has given me much trouble; for if we regard the so-called mouth as the original opening or future anus, the positions of the water-tubes and spines as compared with the same stage in other Echinoderms are wrong. If the opening in question (*mv*) is a mouth or second infolding of the epiblast, where are the intestine and the anus? In his admission * that Apostolides is right in his interpretation of the homology of intestine and anus Metschnikoff must have abandoned the idea that the interpretation of this figure is a correct one so far as the opening *mv* is concerned. I have found a larva similar to the figure quoted (Fig. 6), with the two transparent bodies (*v*) which

* *Zeit. f. Wiss. Zoöl.*, XXXVII. p. 307.

† *Op. cit.*, p. 210.

‡ Studien über die Entwickelung der Echinodermen und Nemertinen, *Mém. de l'Acad. Imp. des Sci. de St. Pétersb.*, VII^e sér. XIV. 8.

§ There is a mistake in lettering and in description. On p. 15 *mv* is spoken of as mouth. *mv* in the explanation of Figs. 3, 4, 5, is the vitelline membrane ("Dotterhaut").

he has interpreted as water-tubes, and I am led to regard it as admitting another interpretation from his. It shows that what he regards as mouth may be in reality the anus. I am not wholly settled in mind, however, in this conviction, especially if the two transparent bodies (v) are, as he interprets them, water-tubes, the right and left vaso-peritoneal vesicles. Their position would lead to the belief that Metschnikoff's interpretation is correct, for in all Echinoderms these bodies are found one on each side of the plutean or brachiolarian mouth. Subsequent larvæ, which are here figured, show that the provisional plutean appendages are not necessarily first formed at the anal pole, as these are situated in the larva he figures.

Mouth, Œsophagus. — The mouth (or) of Amphiura is formed by invagination. I was in doubt when I wrote my preliminary account of the development of Ophiopholis whether the primitive gastrula opening became mouth or anus of the pluteus. My figures* seem to indicate that the gastrula mouth becomes the plutean mouth; and if that is true, Ophiopholis is certainly exceptional. I find the same difficulty in the study of the development of Amphiura, although it seems as if the general law* of Echinoderm development ought to hold here as in Strongylocentrotus and others. In a bisymmetrical larva of Amphiura (Pl. II. Fig. 4) we have œsophagus, stomach, and intestine well developed. If there is in this

* *Op. cit.*, Pl. I. The law referred to is that the first opening, blastopore, is the future anus, and a second opening is found to develop into the pluteus mouth. This law has been found to hold in several genera of Echinoids, but has not been supported by observations of the Ophiurans. The supposition has been that in Ophiurans the law is the same as in Echinoids. Observations are now wanting to prove that such is the case. In my paper on the development of Ophiopholis it was not possible for me to prove that the gastrula mouth, blastopore, becomes the vent of the pluteus. The lettering *gm* (Pl. IV., *Bull. Mus. Comp. Zoöl.*, Vol. XII. No. 4) of the gastrulæ of Echinarachnius is a typographical error, as a reference to my text will show. In some other Echinoids the blastopore becomes the vent of the pluteus, according to most authorities. I have not observed the fate of the blastopore in Echinarachnius, and this erroneous lettering might imply that I was sure that the blastopore becomes the pluteus mouth. The candid reader of my text (pp. 128, 129) will I hope acquit me of holding that the blastopore becomes the pluteus mouth in Echinarachnius. Of the origin of the mouth of the pluteus it is said (p. 128): "The walls of this infolding" (second invagination) "break away and form the future anus (v) of the stages immediately following the gastrula, and probably the mouth of the pluteus." Of the fate of the blastopore in Echinarachnius I have no observations, and "nothing to show that there is any difference in this genus from what is recorded in Strongylocentrotus and other Echinoids" (p. 129).

larva an anal opening into the intestine, that opening would be functionally useless, for it is closed by the sac in which the embryo hangs. Before the young sever their attachment to the parent, anus and intestine are atrophied or highly modified so as to lose all semblance to these organs in other Echinoderm larvæ. The mouth also in very early stages, as can be observed by an examination of Figs. 5, 7, is closed by the sac in which the larva is suspended. It would not seem strange if, in the possibly abbreviated development which is found in Amphiura, a true anal opening never forms, and that the primitive gastrula cavity is formed not by invagination but by delamination. The intestine and anus in stages corresponding to Fig. 4 are not figured by Metschnikoff.

For a considerable time, and almost through the whole course of the development of the bilateral embryo, a conspicuous cluster of orange pigment is found at the anal pole of the larva near the intestine.

There are some difficulties in a comparison of the bilateral larvæ (Figs. 4–11) with others which have been figured by other observers. In the papers by Apostolides and Metschnikoff the position of figures of the same larva is different, and Metschnikoff does not follow in his figures the orientation given in the text. He says:* "Wenn man sich den Embryo mit dem Œsophagus nach oben, den Magen nach unten liegend denkt, so wird sich die Wassergefüsssystem Anlage auf der linken Seite befinden." This is a position exactly opposite that in which he has placed his figures. As the mouth on a median line is a convenient point for reference, its position ought to be mentioned when speaking of the position of the larva. When the mouth is turned to the observer and the anal end of the larva is above, the right water-tube (right-hand side of larva) is that which divides into five divisions. When the mouth is turned from the observer and the anal pole placed above, the left water-tube is that which divides to form the water-vascular system.

Umbilicus. — The connection of the bilateral larva with the ovary is by means of a structure which may be called the umbilicus, or "Nabelschnur" (*u*). It is at first, in young larval stages, broad and thick, and later becomes reduced in size to a simple string-like structure. Its existence prior to the pentagon-shaped larva is not indicated by Apostolides and Metschnikoff, although represented by Max Schultze. Metschnikoff† says: "Erst auf solchen Stadien (Fig. 17) könnte ich deutlich den von Krohn und Max Schultze bereits gesehenen Strang beobachten welcher sich dem das provisorische Skelet tragenden Körpertheile des Embryo inserirt." In the early conditions (Figs. 5, 8, 9) of the bisymmet-

* *Op. cit.*, p. 16.

† *Op. cit.*, p. 18.

rical larva it is present, but has been ruptured in the young larvæ which he has figured prior to that represented in Fig. 17, and will be seen figured in my plate in some of these or corresponding stages.

Of the ultimate fate of the "Nabelschnur" (*u*) Metschnikoff says: * "Da er über schliesslich (ebenso wie das provisoriche Kalkskelet) verschwindert, ohne in den Körper des sich bildenden Sternes direct überzugehen, so muss man seine Rückbildung durch Atropie annehmen." That a part of the umbilicus and the whole of the provisional skeleton of the pluteus is absorbed seems to me true, as traces of the provisional skeleton (*ps*) are found in the pentagonal larva even when free from the mother. Of the freedom of the oldest stage when the remnant of the plutean skeleton was observed there may be doubt; but there can be little question that this skeleton enters into the formation of the future starfish, although possibly not directly into the formation of any special organ.

It is thought that all the "hunchback" part † of the larva figured in Fig. 7 passes by absorption into the embryo.

As to what part of the bisymmetrical larva is the homologue of the pluteus of Ophiopholis it may be said that the Amphiura young is a pluteus without arms, although the calcareous framework of the lateral arms is present. The larva (Fig. 7) is a pluteus with aborted arms.

Water-tubes and "Lateral Scheiben." — In the early stages of growth up to the pentagonal larva the water-tubes (Hydrocœlen) and the lateral bodies (Enterocœlen) were seen, but nothing new added to our knowledge of these structures. In one larva the right-hand water-tube is present after the left has begun to push out the five extensions which form the terminal tentacles. This tube was thought to open externally, and near its opening a trifid calcification was observed. It is known that monstrosities so called in the development of the tubes are said sometimes to give us a larva with even a pentamerous right water-tube, and it may be that this development belongs in this category. It does not seem reasonable that the right-water vesicle disappears, as stated by Metschnikoff. ‡ We must wait in answer to the question of the fate of the right vesicle until we know the origin of the right "Scheibe," or enterocœl.

Observations upon the origin of the water-tubes of the Ophiurans are very much needed in the present state of science, and we can hardly put

* *Op. cit.*, p. 18.

† The protuberance on the right-hand upper corner of the figure imparts to the larva a hunchbacked appearance, All of this protuberance is absorbed in the growth of the young Amphiura.

‡ *Op. cit.*, p. 16.

great confidence in some of the speculations which have been indulged in until we know whether the Enterocœlen, and the Hydrocœlen or water-tubes, originate in Ophiurans as paired structures or not, and whether the right Enterocœl is the same as the right "Lateral Scheibe" of Metschnikoff or not. The question also of the connection of the water "tubes" with the oral plate or madreporite is also imperfectly answered. It may be supposed that the Hydrocœlen form from the Enterocœlen, which are themselves diverticula of the first invagination, and which persist in the form of the "Lateral Scheiben."

Provisional Spines of the Pluteus. — Max Schultze * first made the interesting discovery that the embryo of the viviparous *Amphiura squamata* is furnished with a provisional calcareous skeleton which is comparable with the spines of the arms of a pluteus. This important discovery has been verified by several observers. It presents us with a most interesting case of the retention of structures useful to free larva in an embryo where they can have no use, or if they have any use it must be a somewhat different function from that which they have in the free pluteus.

The provisional spines of the pluteus have a maximum development in the bisymmetrical larva (Fig. 8), but are not wanting in the younger stages of the pentagonal embryo, where they are very much reduced in size. The number, mode of origin, and position of the provisional spines of the pluteus seem to differ in different specimens. They are not always double or bisymmetrically arranged in reference to a plane passing through the mouth of the symmetrical larva and the umbilical connection with the parent. In the majority of instances the spine on the side opposite that in which lies the "left water-tube" is well developed, while that on the same side as the left water-tube is stunted (see Figs. 6, 7).

The provisional spines generally originate near the anal pole, but are found in some larvæ in the vicinity of the stomach and on one side of the body (Fig. 4, *ps*). In older stages of the bilateral larva the provisional spines form by reticulation a calcareous network (Fig. 10) similar to what we find in the anal lobe of Echinarachnius. This reticulation is hardly distinguishable from the permanent radial plates which form in the same position on the larva. The provisional calcareous rods are ultimately absorbed in the developing embryo, but do not wholly disappear until after the young Amphiura has passed into the pentagonal form (Fig. 13). When last observed they were noticed just under the region of the

* *Op. cit.*, pp. 44, 45; Pl. I. Figs. 2, 3, 4, 5 *a*. Krohn was not able to find a trace of the pluteus (*op. cit.*, p. 340).

body where the umbilicus is joined to the edge of the disk (Fig. 12). Metschnikoff has figured them in the same position in Fig. 17 of his Plate IV. There seems abundant evidence that they are absorbed into the body of the forming Ophiuran, as in Ophiothrix and Ophiopholis.

III. THE PENTAGONAL EMBRYO.

There are two forms or conditions in which the pentagonal embryo is found. The one (Fig. 12) of these follows in age close upon the bilateral larva, and is still attached to the mother; and the latter is represented by those larval stages when the young Amphiura has severed its connection with the parent and is leading an independent life (Fig. 13). The exact time at which the umbilicus is broken was not observed, but the rupture takes place certainly a relatively long time before the young leaves the parent. The young larva then seems for some time to live free in the parent without umbilical connection.

It becomes an interesting physiological question to determine the mode of alimentation of a young Amphiura in the body of the parent, and with no real connection with the adult. It would seem as if in older stages at least the young might be nourished by foreign matter taken into the open mouth. The genital slits of the parent would furnish an easy entrance for foreign bodies or small animals into the sacs, and the young Amphiuræ while free in the body of the parents probably use these bodies as food.

A. THE DISK.

1. Plates of the Abactinal Region of the Disk.

Dorsocentral and Radials. — The aboral integument of the disk has embedded in it in young stages of growth six reticulated calcareous plates. These plates consist of a single central, dorsocentral (*dc*), and five radials, the primary radials or radialia (*rp*). These plates have been observed, figured, or described by Krohn,* Schultze,† Lyman,‡ A. Agas-

* *Op. cit.*, p. 341. Krohn figures (Pl. XIV. Fig. 1) a cross-shaped dorsocentral surrounded by a continuous calcareous ring with no separate radials. This "einzigen Stücke bestehende Kalknetz" gives rise to "fünf Schuppen." The radials, according to a note on this page, are isolated from the beginning.

† *Op. cit.*, p. 41.

‡ Ophiuridæ and Astrophytidæ, Old and New, *Bull. Mus. Comp. Zoöl.*, Vol. III. No. 10, p. 264.

siz,* Metschnikoff,† and Ludwig.‡ The dorsocentral early takes its permanent place, and remains near the centre of the abactinal region of the disk; the radialia are subsequently to formation pushed nearer the periphery by the interposition of new plates between them and the dorsocentral. They are never, however, in Amphiura pressed to the very periphery of the body, and consequently never extend out on the arms. In early stages the dorsocentral § is not formed, the five radialia originating first.

The dorsocentral in the young Amphiura (Fig. 13) occupies the centre of the abactinal surface of the body, and is irregularly pentagonal. Its origin was not traced, but there is no reason to question the observations of Ludwig‡ and Schultze|| that the radials appear before the dorsocentral. In the youngest pentagonal embryo which was studied (Fig. 12) in which the umbilicus (*u*) was still unbroken, the five radialia (*rp*) were well formed and of comparatively large size, while the dorsocentral (*dc*) was small, indicating apparently a later formation. Ludwig‡ says, "Ganz unterdrück aber wird die Entwickelung eines Centrale niemals." The radialia or primary radials are among the first plates to form, and originate while yet the Amphiura is in a bilaterally symmetrical condition. It is extremely difficult to distinguish them in earliest conditions from the network at the anal end of the provisional pluteus rods (Fig. 8), but they are among the first plates of the Amphiura to form. The question of whether they antedate in formation any of the plates of the actinal region of the disk will probably be correctly answered in the affirmative. They probably appear before the first pair of adambulacral (*q. v.*) plates and undoubtedly before the terminalia (*q. v.*).

A. Agassiz states:¶ "We have the most positive proof of the origin of the dorsocentral plate of starfishes and Ophiurans as a single Y-shaped rod appearing simultaneously with the five basals." Ludwig, on the other hand, states: "Diese sechste Platte, das Centrale tritt bei *Amphiura squamata* in der Regel später auf als die fünf Radialia." Ludwig holds**

* Embryology of Echinoderms, *Mem. Amer. Acad. Arts and Sci.*, III. 1856.

† *Op. cit.*, p. 18; Pl. IV. Fig. 17.

‡ *Op. cit.*, p. 195.

§ The reader is referred in this connection to Fig. 16, Pl. VII., in my paper on the development of Echinarachnius (*Bull. Mus. Comp. Zoöl.*, XII. 4). In this figure, which is of a young sea-urchin, the calcareous network of the dorsocentral plate (*c pl*) has not begun to form, although that of the ring of plates surrounding it is well marked.

|| *Op. cit.*, Pl. I. Fig. 4.

¶ Report on the Echini, *Mem. Mus. Comp. Zoöl.*, Vol. X. No. 1.

** Page 187.

that the terminals appear at the same time as the radials, but could not determine whether their origin is earlier or later in time. He considers it probable that the terminals appear earlier. It is suggested that they appear in Amphiura * later, as their comparative sizes (shown in my figures) indicate. It is believed that Ludwig is right in his statement that the centrale (dorsocentral) appears later than the five primary radials in Amphiura.

It is interesting to see how far this order of late development of the dorsocentral is repeated in plates of the Asteroidea and Echinoidea supposed to correspond with the dorsocentral, radials, and terminals. Our knowledge of the sequence of the development of these plates is hardly accurate enough to make definite statements, but there seems to be some resemblance in these three groups in this particular.

According to A. Agassiz,† the abactinal system of the young Echinoid "consists of a single large plate, . . . and the new plates are added in a spiral manner round the anal plate." This large abactinal plate is figured in Fig. 28 † and in several figures by Lovén. It would appear from this that they regard ‡ the suranal plate as formed in sea-urchins of this age before the oculars and genitals. A. Agassiz finds in Salenia an adult genus with this plate, as in the young of some other genera; and according to Lovén, § in this genus (Salenia) this plate is retained through life, and instead of being a temporary is a permanent structure. A. Agassiz ‖ has examined specimens of young Saleniæ to obtain information in regard to the suranal plate and its homology with the "single large anal plate of the early stages of young Echini belonging to other families;" but he finds that "the arrangement of the plates of the abactinal system does not differ from that of the older specimens, the suranal being only pro-

* Sladen (*op. cit.*, p. 27) judges from the figures of larval Ophiurans which pass through a pluteus stage, given by Agassiz, Metschnikoff, and Müller, that it is more probable that traces of the terminal plates appear before the first radials. In the case of the Amphiura studied and figured by Metschnikoff, and possibly from the figures of Müller, he finds the reverse seems to occur. My observations on *A. squamata* show that the radials are well formed before the terminals attain any great size, or that the radials are of considerable size before the terminals have grown from a simple spicular form.

† Embryology of Echinoderms, *Mem. Amer. Acad.*, IX. 1864, p. 12, Fig. 28.

‡ Revision of the Echini, *Mem. Mus. Comp. Zoöl.*, p. 280, Pl. IX. Figs. 3, 6, 7, 8; Pl. X. Fig. 2.

§ Études sur les Échinoïdées, *Kongl. Svenska Vetenskaps Handlingar*, Bandet 11, No. 7.

‖ Report on the Echini, *Mem. Mus. Comp. Zoöl.*, Vol. X. No. 1.

portionally smaller." This fact has possibly a meaning in the comparative time when the suranal (dorsocentral) is formed, as compared with the ocular and genital, as will be spoken of directly.

In regard to Neumayr's statement that in the young "Glyphostomes" the anal plate is first formed, and that the plates of the genital ring are later detached from it, A. Agassiz * states that undoubtedly the anal plate in young Echinoids is the first plate to appear, and that genital and ocular plates are independently formed around it.

Our interest in the study of the dorsocentral plate of Amphiura is connected intimately with the origin of the suranal plate of the Echinoids. In Echinoids of some genera, according to the authority mentioned, the abactinal region is covered by a large single plate, suranal, which is possibly the dorsocentral, while in Amphiura a plate believed to be homologous, dorsocentral (*d*), is very small in young stages, and is thought to be developed *after* the radials. While opinions may be divided as to the homology of the primary radials in Amphiura with ocular and genitals of sea-urchins, it would seem as if a uniformity of opinion might be arrived at in regard to the dorsocentral. If, however, in Echinoids this plate forms before the ocular and genitals, and in Amphiura after the same, one is tempted to ask whether they are homologous. One might, of course, avoid the difficulty by the truism that the relative time of development is of little consequence, and that the appearance of the plate in Amphiura is simply retarded. Such an escape from the difficulty does not give much satisfaction, even if we remember the abbreviated development of Amphiura. The theory that the dorsocentral of Amphiura is homologous to the suranal of sea-urchins is believed to be true. As far as any objection based upon the different time of appearance of this structure is concerned, it is first necessary to examine the observations adduced in its support.† While the evidence seems to be against the late formation of the dorsocentral in Echinoids, the author is confident that in one genus of Echinoids, viz., Echinarachnius, no single plate centrally placed, which represents the suranal, is developed before plates regarded as homologous to the oculars and genitals. He believes that the suranal, which

* Report on the Echini, *Mem. Mus. Comp. Zoöl.*, Vol. X. No. 1, p. 33.

† It is believed that the difference in relative time of the appearance of the dorsocentral, and the ten plates around it, in Strongylocentrotus and Amphiura cannot be satisfactorily studied except from stages of the former genus much younger than those figured by Lovén for this purpose (*op. cit.*, Pl. XXI.). There is a call for a study of the young sea-urchin, between these and the pluteus, before we can definitely state whether dorsocentral or the ten surrounding plates first appear, or whether they appear simultaneously or not.

is here regarded as the dorsocentral, is developed after the oculars or genitals,* and that the dorsocentral is formed axially to the same. In Toxopneustes, according to authority mentioned, the facts seem to be diametrically opposite those mentioned for Echinarachnius, while the last-mentioned genus resembles Amphiura so far as the time of the development of the dorsocentral is concerned.

The dorsocentral of the starfish, Asteracanthion, is apparently formed in some cases after the radials (oculars) and genitals. In Asterina the dorsocentral seems to coexist with the other ten plates from the first, as shown in Ludwig's figures, although he does not say whether the dorsocentral appears before or after the other ten. Lovén's figure of the young *A. glacialis* (*op. cit.*) is not young enough to answer our question. In A. Agassiz's Embryology of Asteracanthion it is shown that the ten calcareous rods are the first to form, and attain a considerable size before the dorsocentral is represented. Metschnikoff gives very instructive stages † of the young of an unknown Asterid ; but his description is so short, and the arrangement of plates in it so remarkable, that it would be out of place to interpret them here. This stage and those preceding it give no answer to the question when the dorsocentral is formed. The question which plates in the young Amphiura correspond to the oculars of sea-urchins assumes a new phase in the light of what we know of the permanent retention of the radials in the abactinal hemisome of the body of Amphiura, and the relation of the terminals to the primitive tentacle. Now that we know that the primary radials of Amphiura are not pushed out to the extremity of the rays, but always remain in the disk, and that another

* Consult Pl. VII. Fig. 16, *Bull. Mus. Comp. Zoöl.*, Vol. XII. No. 4. This figure is thought to show the truth of the belief stated. No limestone rods were observed in *cpl*, which occupies the position of the suranal or dorsocentral.

† The figures alluded to are found on Pl. XII. Figs. 1 and 2 (Studien über die Entwickelung der Echinodermen und Nemertinen). Fig. 1 is an abactinal view, with five large peripheral, spiniferous plates, and a madreporic plate (*Mp*). Within this ring of peripheral plates are seven smaller, non-spiniferous plates, one of which is centrally placed. Metschnikoff was unable to determine the genus to which this starfish belongs. He found the absence of the anus to recall Astropecten, Luidia, or Ctenodiscus, but supposes that the character of the spines does not belong to these genera. With this objection, so far as the size and general arrangement of these huge spines are concerned, I cannot agree with him. I have studied the young of our *C. crispatus*, and find the five peripheral plates which he figures, each with three large conical spines, a median and two lateral, on each plate. Between each pair of these peripheral plates, which are regarded as the terminals, there are three adambulacral plates in each interradius, while in the stage figured by Metschnikoff there is but the single madreporite in this position.

set of plates (terminals) do suffer the change, we have this difficulty in a comparison of the young Echinoid with the young Amphiura. The terminals of Amphiura are independent centres of calcification from the radials. If terminals and radials in Amphiura lie in the same radius, how can the one or the other, especially the former, be the same as the oculars of the sea-urchin? If we compare the apical region of a sea-urchin and the abactinal hemisome of the young Amphiura, we have in Amphiura the terminals, plates which are supposed to be the same as oculars of the sea-urchins. If that is so, what plates in sea-urchins can be found to represent the radials of Amphiura, plates which are separate calcifications in both Ophiurans (Amphiura) and Asterina between terminals and dorsocentral? None exist. If, on the other hand, we say the oculars of sea-urchins are the homologues of the radials of Amphiura, they are not the same as another definite calcification, the terminals situated at the tip of the arm. Is it not more logical, from embryological grounds, if we compare the apical system of young Echinoids with the abactinal hemisome of Amphiura, not to suppose the first-formed plate in an ambulacral radius is an ocular homologous to a terminal, but an ocular homologous to a radial; provided, of course, we compare the radial series of Amphiura with the radial series of Echinoids?* Is it possible that what we call the ocular of the sea-urchin is in reality a consolidation of the radial and the terminal, or that a plate homologous to the radial is never developed? Either of these conditions would be a possibility, and more probable than that the eye-plate of the sea-urchin

* By the "radial series" of plates in Amphiura the author means the series which lies in the radius extending from the centre of the dorsocentral through the middle of the primary radials and terminals. By the radial series of the sea-urchins, the author means those plates which lie in a radius extending from the centre of the dorsocentral through the ocular. The above remarks in relation to radials and oculars of Ophiurans and sea-urchins apply to those who compare the terminals of starfishes and brittle stars without pluteus, with the ocular plates of the sea-urchin. Those, on the other hand, who compare the terminals and radials (primary) of Amphiura are believed to have this difficulty. If the terminal of Amphiura is compared with the genital of a sea-urchin, the madreporic opening of the Echinoid, which lies in the same interradius as a genital, ought to lie in the same radius as a terminal in Amphiura. The same objection would hold in a comparison of the radialia of Amphiura and the genitals of sea-urchins; the madreporic body, which in the young Amphiura is found in a plate called the oral, in the interradius would be found in the radius. This, of course, supposes the fact that the genitals and the madreporic body, since they lie in interradii, are comparable, and waives the homology of the so-called ambulacral plates, which Ludwig does not find in sea-urchins except in the auriculæ.

is homologous at the same time to the radials and the terminals which originate in both Amphiura and Asterina in two separate calcifications.

A comparison of the young sea-urchin with the young Amphiura reveals the following fact. The radials (*rp*) of Amphiura occupy a position, as regards the dorsocentral, similar to that which the ocular plates of the young sea-urchin hold to its anal plate, which is regarded as the dorsocentral. In the sea-urchin the ocular plate is perforated for the eye-spot. The eye has not been found in the radials of any Ophiuran. In one case the plate is an ocular, or eye-plate; in the other it has no eye. Nor is the eye known in the terminal in the Amphiura. Is a plate with an eye homologous to one without an eye? This of course opens the question whether the "eye" of the starfish and the "eye" of the Echinus are homologous. I believe an answer to this question can only be given by a histological study of the eye and its relation to the water-tube in Echinoids. A. Agassiz has shown the relationship of the eye-spot to the unpaired tentacle of Asteracanthion, and it remains to be seen whether in Echinoids the eye-spot is similarly formed. When it has been shown that the eye-spot of Echinoids is homologous to the eye-spot at the end of the arm of the starfish, it may be asserted that the terminal plate of the starfish is homologous to the ocular of the urchin. The adult form of the starfish and of Amphiura would imply that the terminal plate or the plate over the eye-spot of the starfish is homologous to the terminal plate of Amphiura, notwithstanding an eye-spot has not been described in any of the Ophiurans. If an association of the eye-spot with a plate means homology of those plates, the oculars of the urchins and the terminals of the starfishes (Ophiurans) are homologous; but if homologous, what plate in the young sea-urchin corresponds with the radial (*rp*) of Amphiura?

From a comparison of the young Amphiura with the young Echinoid it would seem as if a non-ocular (without pigment-spot) plate (*rp*) in the former occupies the same relative position to the dorsocentral as an oculated plate in the latter. Are they not then homologous? From a study of the adult Amphiura and the adult starfish it would seem that the plates (*tp*) at the tip of the ray adjacent in the latter to an eye-spot are homologous. If the terminal plate of the starfish with the eye-spot is homologous to the terminal of an Amphiura, and the plate with the eye-spot is homologous in starfishes and urchins, we are led to suppose the radials of Amphiura to be plates unrepresented in urchins. It seems more natural to compare radials in Amphiura with oculars in sea-urchins, notwithstanding the position of the eye-spot.

According to Balfour,* the central calcareous plate appears after the five radials and the five interradials. From this reference and the others already mentioned, it would appear that in the starfishes, as far as observed, the dorsocentral forms after radials and interradials. On account of a discrepancy in the observations of Thomson and Götte it is difficult to compare the centrodorsal of Crinoids with the dorsocentral of the Ophiuran. It would seem from Thomson's account as if the centrodorsal was a single plate originating after the basals, but Götte holds that the centrodorsal is formed of a number of at first independent rods which arise simultaneously with the basals.

The shape of each of the five radialia may be seen by a consultation of Figs. 13, 14. In the early condition of the plates the calcareous network consists of a somewhat coarse, open reticulation, over which grows a finer network connecting portions of the larger reticulation, and finely knitting the whole together. This second kind of network does not appear in figures of the primary radials and dorsocentral which have been given by others.

The primary radials, as shown by Ludwig, are not pushed out to the end of the rays, as is believed by many naturalists. They always remain on the abactinal hemisome of the body. It is therefore necessary to modify what Balfour says on page 564,* of the formation of the plates of Ophiurans, that "the *original* five radial plates remain as terminal segments of the adult rays." The original five radial plates are believed to be the primary radials of the abactinal hemisome in Amphiura, and are recognized in late stages on the body of the Ophiuran.

Oral Plates. — There are certain plates (Fig. 18 *o*) situated in the interradii, peripherally to the dorsal plates, or radialia at the very rim of the disk, which, although belonging to the actinal hemisome, must be mentioned here. They in point of fact originate on the abactinal hemisome, and by subsequent growth are carried to the actinal hemisome, forming the oral shields. Their position of origin only will be spoken of here, as a description of them will be given in an account of the plates of the month (*q. v.*).

The oral plates originate on the abactinal hemisome in the interradii on the outer margin of the disk. The first, or one of the first, of these to appear is perforated (Fig. 17 *o*), and according to Ludwig,† is a madreporite or oral plate bearing the madreporic opening (see oral plates).

Intermediate Plates. — Certain plates which are next to form on the

* Comparative Embryology (Second Edition), p. 559.

† *Op. cit.*, pp. 196, 197.

abactinal hemisome after the primary radials and dorsocentral, were given by Ludwig the name of intermediate plates. These plates immediately following the primary radials form in the interradii, and may therefore be called interradials or basals. In the line of the radii also there are new plates beginning to form, among which may be mentioned underbasals and radial shields. We shall first consider the basals and interradials.

Basals. — The first interradial plates form on the periphery of the abactinal hemisome on interradii between contiguous radialia. They are triangular in shape, and occupy a triangular interspace between adjoining primary radials. These plates are commonly confounded with the orals, which are forced to the actinal surface of the disk before the interradials arise. The first set of interradial plates may be known as the abaxial basals or first interradials. The next plates to form on the abactinal hemisome after the abaxial interradials are also interradials, and arise in the corners left between the dorsocentral and contiguous radialia. They arise as trifid or quadrifid calcareous spicules, and are five in number. They are not, however, synchronous in origin. Even in this stage, although two rings of interradials are formed, the radialia are not separated from the dorsocentral, and the surface of the abactinal hemisome is mostly made up of the "primary rosette" of plates, the dorsocentral and the radialia. As the growth of the new interradial plates proceeds, the increase in size of the radialia and dorsocentral is not the same as that of the interradials, and the original rosette is more or less contorted in its form. Almost simultaneously with this contortion appear a number of plates, among which may be mentioned a new ring of interradials, five radial plates between the dorsocentral and the radialia, and the radial shields. In the formation of new rings of interradials, at least in the next set of plates, the newly formed seem to lie adaxially to those already developed. The next ring of interradials arises between the last-formed interradials and the periphery of the dorsocentral.

In the case of the radial series of plates, however, the next plates to form after the radialia are the radial shields. These plates are remarkable in more than one way. Anatomically they can be recognized in all genera of Ophiurans, and their mode of development in pairs is exceptional among radial plates of the disk. All abaxial plates thus far formed on the abactinal hemisome have originated singly, one in each interradius, and are five in number. The primary radials and basals follow the same law as far as the number five goes. The radial shields are the first in the abactinal hemisome to originate in pairs. On the actinal side we shall find all plates originate in pairs except the *tori*, or jaw-plates ; but on the abactinal side of the disk the plates which ultimately form radial shields are the first bodies to arise in this way. The radial shields lie just abaxially to the radialia, one on each side of a radius. In one instance, and that in the preparation figured, a median radial plate abaxially placed to the radialia had formed before the radial shields began to appear. In other specimens that was not observed to be the normal method of formation. I have figured this specimen from its similarity to a larva figured by Lyman,* about which more will be said later when considering the homology of the radial shields. It is not until the radial shields have reached some size that a radial plate is formed between each of the radialia and the dorsocentral on the lines of the radii. This last-mentioned plate, the underbasal,† tends to separate the primary radialia and dorsocentral, and from the first their edges do not join each other.

The interpolation of new plates in the abactinal hemisome now becomes more or less irregular. If any law for the formation of these plates exists, the modification in size of the plates renders it extremely difficult to trace it in their formation at this time.

The nomenclature of the intermediate plates on the abactinal hemisome is similar to that given by P. H. Carpenter in his discussion of Crinoidal and Ophiuran morphology.‡ It seems to me, however, that it would have been better, in considering the relationship of the basals in the young Amphiura and their homologues in the projection of the calyx of an Antedon larva, for Carpenter to have introduced, instead of his Fig. II. (a copy of one of Ludwig's figures), a copy of another (Fig. 25) of the same author. In this figure (Fig. 25) there is but one circle of interradial, intermediate plates and no "underbasals," while the intermediate plates of Ludwig's Fig. 25 and Carpenter's diagram of the Antedon (Fig. III.) numerically correspond. The additional intermediate plates, both radial ("underbasals") and interradial ("basals"), in the figure by Ludwig, which he (Carpenter) has chosen for Fig. II., lead to a difficulty in one particular in a comparison of the young Amphiura and Antedon. It is an important thing to know whether the intermediate plates of Ludwig's Fig. 25 are the same as the Plates 3 of Carpenter's diagram (*loc. cit.*, Fig. II.).

* Challenger Ophiuroidea, Pl. XL. Fig. 11, p. 157.

† Notes on Echinoderm Morphology, No. V. On the Homology of the Apical System, with some Remarks upon the Blood-vessels. *Quart. Journ. Micros. Sci.*, Vol. XXII. The homology of this plate with the Crinoidal underbasal is recognized by Carpenter.

‡ Notes on Echinoderm Morphology, No. V. pp. 10, 11. *Quart. Journ. Micros. Sci.*, Vol. XX.

This question can be answered in part by a knowledge of whether the ring of interradials just abaxially or outside of the so-called basals (3) are earlier or later in formation than the basals (3). They appear to be later, for in Ludwig's Fig. 21 we have a single interradial plate just beginning to form between an abaxial and an adaxial interradial (the abaxial is probably the oral). Moreover, this seems to be the mode of formation referred to by Ludwig in the words, "Es scheiben überall im Bereiche des dorsalen Scheibenperisoms neue Intermediarplatten zwischen und neben den einmal gebildeten sich anlegen zu können." If the intermediate plates are formed later, the Plate 3 in Carpenter's Fig. II. would be the same as one of the ring of interradials in Ludwig's Fig. 25, which exactly corresponds with the basals (3) of the projection of the Antedon larva.

The determination of the relative length of the arm when the underbasals and basals appear may be made by considering the relative development and number of pairs of the adambulacral plates. Carpenter states:* "The radials of the young Amphiura do not long remain in contact with the dorsocentral; for by the time that *two* adambulacral plates have appeared between them and the terminals they are separated from the dorsocentral by the rudimentary basal plates, while underbasals are developed shortly after." In the figure quoted (Pl. I. Fig. 12) by Carpenter in this connection, which is probably a little older than one necessary to illustrate the above statement, three *pairs* of side arm-plates (adambulacral) are figured between the terminal (T) and the primary radials (4). Two pairs of lateral arm-plates at least are developed before the plates which Carpenter calls basals appear. It is taken for granted that the lateral arm-plates are considered adambulacral by Carpenter, — a homology of which there is little doubt, — and must be the ones referred to by him, since they are the only plates, in the figure quoted by him (Pl. I. Fig. 12), between the terminals (T) and radialia (4).†

The homology of the radial shields of the Amphiura with the first brachials of the Crinoid would seem not unreasonable.‡ The only paired plates of the arms with which they could be compared are the adambulacral. With these, however, they have little resemblance save in their double origin.

* On the Apical System of the Ophiurids, *Quart. Journ. Micros. Sci.*, Vol. XXIV., Jan., 1884, p. 6.

† The first and second adambulacrals lie on the oral side of the disk, and cannot be those referred to by Carpenter as appearing *between* the terminals and radials.

‡ This suggestion is believed to be original, although it is a direct sequence of the adoption of the theory that the radials of Amphiura and of the Crinoids are homologous, as shown above (adopted from Carpenter and others).

Lyman * gives two very instructive figures of the young *Hemipholis cordifera*, from which he draws the following conclusion: "It thus appears that radial shields so nearly universal among Ophiurans are not special plates, but entirely homologous with other disk-scales, and by no means the first to appear." In the younger of these two stages of the young Hemipholis there is a dorsocentral surrounded by five radial plates and an outer circle of five interradial, while there are ten arm-joints. The development of the basal plates must be very much more retarded in this genus than in Amphiura; for in the latter, with half the number of arm-joints and many more interradial plates, the radial shields and some other plates have appeared. The second figure (Fig. 11, *op. cit.*) of a young Hemipholis older than the last is very interesting. In it there is a dorsocentral surrounded by five radials. In each of the interradii there are three interradial plates. There is a second radial beyond, abaxially to the primary radial. Peripherally placed to the second radial are radial shields, one on each side of the radius. The condition here is about the same as that which we find in an Amphiura in which the development of the arms is very much less (Fig. 19) than in Hemipholis. Every observation would probably agree with the above-quoted statement of Lyman, that the radial shields are not the first to appear; and it is thought that they are the same in mode of origin as the dorsocentral, radialia, or interradial plates. The radial shields arise before the underbasals, which are the only other plates in the radii in this early condition. They are the first of the radial series to arise abaxially to the radialia.

2. Plates of the Actinal Region of the Disk.

The plates of the mouth originate early in the development of the young Amphiura. The so-called V-shaped plates (ad^1, ad^2), described below as the first and second pair of adambulacral, are among the first to form, and can be seen as trifid calcareous bodies in the bilaterally symmetrical embryo (Figs. 7, 8, 10). Although I have not directly fol-

* Report on Challenger Ophiuroidea, Pl. XL. Figs. 11, 12, p. 157. As stated elsewhere, the young Ophiurans clinging to the arms of Hemipholis (Ophiolepis) were observed by Stimpson many years ago.

The younger stages in the formation of the plates in the young Hemipholis would offer an interesting subject for investigation for those naturalists who work in localities where it is found, as from a comparison of Lyman's figures of the young with those here given of Amphiura it is suspected that there is considerable variation in the two genera in this particular.

lowed them back to this larva, from a study of my figures and a comparison with Metschnikoff's Fig. 16, there seems abundant evidence that they precede all other plates of the actinal region of the disk. There is also evidence that they antedate the formation of the terminals, although they are probably formed after the radialia or primary radials.

Metschnikoff,* in speaking of the plates of the actinal region, says that the five parts of the skeleton on the ventral surface of the embryo represent the future jaws. Apostolides † also describes five V-shaped plates. There are really five *pairs* of these plates in early stages, and ten pairs in later conditions when both pairs of adambulacral plates are developed.

The following plates will be considered in our discussion of the mouth skeleton :

1. Adambulacral ; first and second pairs, ad^1 and ad^2.
2. "Ambulacral ;" spoon-shaped plates, *os*, *spl.*
3. Oral ; mouth-shield ; madreporite, *o.*
4. *Torus angularis ;* jaw-plates, *to.*
5. Teeth, *t.*

Adambulacral Plates. — There are two pairs of adambulacral to be considered in this connection, known after Ludwig as the first (ad^1) and second (ad^2) pairs. They are both regarded as homologous to the side plates (*lp*) of the arms, which will be later described. The adambulacrals originate in pairs, five in number. The first pair (ad^1) support the *torus* (*to*). Both pairs are early formed in the development of the actinal hemisome.

First Pair of Adambulacral Plates. — The double origin of the "V-shaped" plates has been shown by Ludwig, and is evident from the figures of Max Schultze (Figs. 5, 6) and Metschnikoff. Apostolides † writes : "Les premières grandes plaques calcaires qui apparaissent avant même que le bras soit à peine ébauché sont les *cinq* pièces fourchues de l'adulte ; il est facile de se convaincre de leur apparition primitive, grâce à leur forme en V et la disposition des tentacules buccaux que

* *Op. cit.*, p. 18. The lettering *cc*, in Metschnikoff's Figs. 11, 12, 13, 16, and 17, Pl. IV., does not refer to the same structures as *cc* in Fig. 6, Pl. III. *cc* in Fig. 16 is an adambulacral plate ; in Figs. 11, 12, 13, and 17, it is a terminal, and in Fig. 6, Pl. III., it is one of the provisional pluteus plates. The rods *cc*, in Metschnikoff's Pl. IV. Fig. 16, are probably the first and second adambulacral. The following corrections may be made in "Selections from Embryological Monographs, Echinodermata" (*Mem. Mus. Comp. Zoöl.*, Vol. IX. No. 3, Pl. III.): *cc*, Figs. 9, 10, 11, and 14 are probably terminals ; in Fig. 13, *cc* are adambulacral, and not provisional limestone rods homologues of the pluteus rods.

† *Op. cit.*, p. 213.

nous avons mentionnée." On page 132 he writes: "On admet que ces pièces fourchues sont formées par la division d'un ossicule discoïde sur la ligne médiane, et la déviation de chacune des deux moitiés, jusqu'à la rencontre de la moitié correspondante du disque voisin à laquelle elle se soude." In these descriptions it seems probable that Apostolides refers to the first pair of adambulacral and possibly the second pair also. It can hardly be supposed that he refers to the first pair of ambulacral, which are later described by me as the spoon-shaped plates after Ludwig, since these never have a V-shape. Whether he refers in his description to the first ambulacral or the first adambulacral (with the second), it may be borne in mind that neither has been formed by a division of a "discoid" ossicle, nor are they ever five in number. The members of the five *pairs* of adambulacral as well as of ambulacral originate as ten separate calcifications. In the youngest condition (a stage a little younger than Fig. 17) of the growth in which they were observed the first pair of adambulacral plates were formed although the terminals were very small. I am therefore led to suppose that the first pair of adambulacrals appear before the terminals. In this embryo (Fig. 17) the pentagonal form is but obscurely indicated. The first pair of adambulacral are portions of the "maxillæ" of Metschnikoff's figure (Pl. IV. Fig. 18, *cc*).

The first adambulacral plates originate in pairs about the mouth (Fig. 15). In early conditions they lie more in those axes which later become the interradials, although they arise before the young has passed into conditions in which either radii or interradii can be definitely recognized. In Ludwig's Fig. 23 they are smaller than the terminals, but in some of my preparations they are larger.

In a later stage (Fig. 17), in which the rays have begun to push out, the first pair of adambulacrals assume a more or less irregular crescentic form, with concave edges turned to the radii. By a continued growth the adradial edge of these plates begins to approximate so that plates of adjacent pairs approach each other. This approximation is confined to about half their interradial border. The adradial half of the rude crescent extends to the mouth opening. By the approach of two of these first adambulacral plates (ad^1) which lie in different pairs, a V-shape is given to the combination. The plates however are free along the line of the interradii. The double network of these plates appears as in the radialia (Fig. 18, *rp*).

Of the homology of these plates with the adambulacral there seems no doubt. I believe also that Ludwig's comparison of them to the side plates of the arms is a correct one, and borne out by their mode of formation as compared with the first ventral plate of the arms, as will be explained in a subsequent explanation of the formation of the ventral plates.

Second Pair of Adambulacral Plates. — The second pair of adambulacrals (ad^2) arise after the first pair, aborally to the same, and are situated more on the interradius than the first pair. These plates also differ from the first pair in the possession of appendages in the form of club-shaped spines. These spines are free at one extremity. The fact that the second pair of adambulacral plates as well as the side plates of the arms have spines would incline one to believe that they are homologous to each other. The second adambulacral plates are ten in number, in five pairs, and with the first adambulacral are among the earliest plates to form.

In Fig. 17 there will be seen between each pair of terminal plates (tp), on the periphery of the disk, two knob-like structures which extend beyond the edge of the disk. These did not escape the attention of Max Schultze,* who described them as extending beyond the disk as "keulenförmige Fortsätze." Ludwig † has also described these bodies, and recognized their resemblance to spines. They were purposely omitted by him from his figures. I think this omission is unfortunate, as they confirm a theory of the relationship of the second adambulacral plates which Ludwig supports, that these plates are homologous to the side plates of the arms. He says : ‡ "Bezüglich der Homologie der Seitenplatten am Arme der Ophiuren mit den Adambulacralstücken der Seesterne kann ich auf meine früheren Ausführungen verweisen und brauche wohl kaum zu bemerken, dass diese Homologie auch in den eben erwählen entwickelungsgeschichtlichen Thatsachen eine Stütze findet." The position of the second pair of adambulacrals so called, and the club-shaped appendage seem to refer these plates to the same category as the side plates of the arms, and make them homologous with adambulacral plates elsewhere among stellate Echinoderms.

The club-shaped appendages lose their relatively large size as the growth of the arm goes on, and it is only when the terminals are just beginning to be pressed out from under the radialia that their projection beyond the edge of the disk is noticed. These club-shaped spines can be seen by looking at the young Amphiura from the abactinal as well as the actinal regions.

Ambulacral Plates. — Of the plates which have been referred to the

* *Op. cit.*, Pl. I. Fig. 5 *c*, Fig. 6 *d*, p. 42. † *Op. cit.*, p. 194.

‡ *Op. cit.*, p. 189.

ambulacral series, there are two pairs which may be considered in the account of the plates of the actinal region of the disk of the young Amphiura. The former of these, or the adoral pair, are known as the spoon-formed plates (*spl*); while the second, partially concealed from view in some of my figures, form the ossicles which complete the calcareous ring of the mouth. The spoon-shaped plates may be known (following Ludwig) as the first pair of ambulacral; the second as the second pair of ambulacral. The former are superficial in their position; the latter more profound. Both resemble each other in their paired origin.

Spoon-shaped Plates. — If we study a young Amphiura in which the pentagonal form has been donned (Fig. 15), there will be noticed in the radius near the mouth opening and between adjacent pairs of first adambulacral plates two elongated reticulated plates placed side by side. These plates are commonly pointed on the adoral ends, more spatulate at the other extremities. They originate early in the growth of the embryo, and in young stages are equal in size to the first pair of adambulacral. The increase by growth of the first pair of adambulacral plates leaves, however, the spoon-shaped plates smaller than the adambulacral. Their position leads to the theory that they belong to the ambulacral series, and their mode of origin does not disprove what their position teaches; but it may be doubted from their want of connection with the first pair of adambulacral plates in early conditions (*vide infra*) whether they are "ambulacral plates."

Second Pair of Ambulacral Plates. — The aboral radial ends of the first pair of adambulacral plates of adjacent pairs of these structures are knit together by two plates which are classed as the second pair of ambulacral plates. These plates form the radial part of the circumoral calcareous ring, and occupy the same position as regards the first pair of adambulacral plates as the arm-joints do to the side plates of the arms.

That the second pair of ambulacral plates are ambulacral in their homology is not doubted, but the fact of their union with the first pair of adambulacral has led me to doubt whether they were not the *first* pair of ambulacral instead of the second. There seems much to support this theory, for it brings all the ambulacral plates whether of the disk or arms into harmony; viz., an ambulacral plate is joined to a corresponding adambulacral. The spoon-shaped plates not only show an exception in their superficial position, but also in early condition are not joined to the first pair of adambulacrals. Although for convenience they are in this paper designated as the second pair of ambulacral plates, it is not wholly clear to me that they are not in reality the *first* pair, and that the spoon-shaped plates are not ambulacral. If the spoon-shaped plates are ambulacral, they are highly modified.

The manner of growth of the ambulacral plates has been carefully described and figured by Ludwig, and I have little to add to his account.

They originate in pairs one on each side of the median line of the arm in a deeper region of the arm on the ventral side. In their earliest form they appear as trifid spicules or small parallel bars. These two members of a single joint unite over the median line, forming by coalescence the solid arm-joint. The union of the separate calcifications has been well figured by Ludwig. The union takes place at first on the adoral and aboral ends, so that in a half-formed arm-joint a median unclosed opening remains after the junction of the two ends. The body thus formed is at first much longer than broad ; later it becomes discoid, when the consolidation is complete.

The distinction between ambulacral and lateral arm-plates is recognizable from very early conditions, and the former are well consolidated before union with the lateral plates is effected.

That the ambulacral plates of Ophiurans are spurs of the side plates was questioned by Lyman,* from his study of certain lower genera of deep-sea Ophiurans, Ophiothelia and Ophiohelus. The separation of the two members which compose one of these "arm-bones" even close to the tip of the arm affords a difficulty in accepting the theory of some naturalists that they originally formed as spurs from the small lateral plates. The development of the plates in Amphiura shows that the arm-joints, "ambulacra," and lateral arm-plates not only originate in two separate calcifications, but also that they have great similarity to the permanent plates in such a genus as Ophiohelus. Attention has been called by Ludwig to the resemblance of the unconsolidated ambulacral plates of Amphiura and the same plates of the deep-sea Ophiuran Ophiohelus. Lyman first suggested the embryonic nature of the unjoined arm-joints of Ophiohelus and other genera.

Orals, or Oral Shields. — The position of the first-formed orals (*o*) is an interesting one ; and a morphological interpretation of their relationship to plates in other Echinoderms is beset with many difficulties, which others have discussed.†

* A Structural Feature hitherto Unknown among Echinodermata, *Ann. Mem. Bost. Soc. Nat. Hist.*, 1880, pp. 3–7, Pl. I. Fig. 12. Report on the Ophiuroidea dredged by H. M. S. Challenger during the years 1873–76, Zoölogy, Vol. V. pp. 237, 238, Pl. XXVIII. Fig. 6.

† Ludwig, Ueber den primären Steinkanal der Crinoideen, nebst vergleichend-

The orals originate near the margin of the pentagonal larva, and have a part of their extent at least on the abactinal side. A single oral which is pierced by an opening is larger than the rest, and is one of the first to form. This is supposed to be the same as the madreporic plate. It is larger than the remaining orals, and like them, by the increase of the plates in the interradii between them and the dorsocentral, is forced in the growth of the disk to the actinal side of the body. In their youngest condition the orals resemble other plates in their spicule-like shape.

The literature written by those who have observed the development of the plates of Amphiura does not agree with Sladen when he says :* "The orals and some of the accompanying plates of the actinal hemisome next appear [after radials and terminals] before any trace of the dorsocentral plate is present." If he means that all the orals appear before the dorsocentral, it cannot have been knowledge derived from what has been published on the development of Amphiura; for Ludwig has said nothing to support such a statement, nor does his figure show more than one oral before the formation of the dorsocentral. On the other hand, Krohn in 1851 and Metschnikoff † eighteen years after figure a well-developed dorsocentral plate before any sign of an oral. It will not be claimed that the figures of the last-mentioned naturalists are perfectly accurate in this particular, for it is believed that the madreporic plate ought to have been represented by them in figures showing the immature dorsocentral, but one cannot suppose that they support Sladen's statement. In Ludwig's Figs. 17, 23, in which no dorsocentral exists, the madreporic plate is formed, but there is no other oral represented. In his Fig. 19, where the dorsocentral is well developed, one of the orals is little more than a three-pronged spicule. Evidently here the dorsocentral has antedated in formation one of the orals. My preparations teach me that the dorsocentral is of considerable size before some of the orals.‡

anatomischen Bemerkungen über die Echinodermen überhaupt, *Zeit. f. Wiss. Zoöl.*, XXXIV. pp. 318–322. Neue Beiträge zur Anatomie der Ophiuren, *Zeit. f. Wiss. Zoöl.*, XXXIV. p. 342. Entwickelungsgeschichte der Asterina gibbosa, *Zeit. f. Wiss. Zoöl.*, XXXVII. Carpenter, *Quart. Journ. Micros. Sci.* XX. (*ns*).

* *Op. cit.*, p. 29. † *Op. cit.*, Pl. III. Fig. 17.

‡ What is said above is on the supposition that Sladen calls the orals the plates (5, Pl. I. Fig. 13), and no others. I think I am just in this supposition. If however he includes among orals the spoon-shaped plates and the adambulacral, as might be done, my criticism above would be unjust, and I gladly withdraw it.

Sladen's paper on the "Primary Larval Plates of Brachiate Echinoderms" devotes some space to the homologies of the odontophore of the starfish. As he does not consider in this discussion the first pair of adambulacral and the spoon-shaped plates

Torus angularis and Teeth. — These structures arise later than the first pair of adambulacral plates, but develop quite early in the growth of the young Amphiura. They form as independent calcifications. The torus is at first an elongated plate or bar, which later becomes semicircular. In Fig. 20 this plate is represented as perforated and reticulated. It appears that the teeth are not separate centres of calcification, but grow out directly from the adoral region of the torus. The calcareous deposit which enters into their formation has the form at first of a reticulated perforated triangular plate.

B. PLATES OF THE ARMS.

The plates of the arms are the following: —

1. Terminals, *tp*.
2. Side plates, *lp*.
3. Ventrals, *v*.
4. Dorsals, *d*.

Terminals. — The terminal plates (*tp*) which lie at the aboral extremity of the arms have been described by many observers. These plates have been confounded by many writers with the radials. Ludwig * first distinguished them from what are already described as the radialia or primary radials. The fact that certain plates early formed in the young Ophiuran were pushed out by a growth of new plates was known, but in all cases these plates were regarded as "primary" plates and were in some instances morphologically misinterpreted. In Amphiura Krohn † has figured the terminal plate, but gives it no special description. Max Schultze ‡ recognized the fact that the terminals belong to the arm proper, and correctly designates them as the "erste Anlage der Arme." A. Agassiz § observed the terminal plates in an Ophiuran, probably Ophiopholis, which he referred to Amphiura. He regards them as the first

of Amphiura, it might be supposed that he does not consider these early formed plates as primary plates of the *test*. In strict language they are mouth-plates, but are so early formed in the larva that they may be regarded as primary plates. As a question of opinion I think they ought to be mentioned in a discussion of the homology of the odontophore.

* *Op. cit.*, p. 187.

† *Op. cit.*, Pl. XIV. Fig. 1, *b*; p. 342.

‡ *Op. cit.*, Pl. I. Figs. 4, 5, *c*. In Fig. 6 they are lettered *f*. He does not seem to have connected Plate *c*, Figs. 4, 5, with *f*, Fig. 6.

§ *Op. cit.*, p. 20, Fig. 32, *y*.

developed dorsal shields (primary radials?). Ludwig * regards this interpretation as incorrect. A. Agassiz has shown that this plate is forced out by growth of the arm to its distal extremity. Metschnikoff † correctly figures the terminalia, and regards them as the "ersten Anlage der Wirbelstücke." The true arm-joints or ambulacral plates, which are regarded the same as the "Wirbelstücke," are formed as a rule in pairs, not medially and unpaired. Ludwig ‡ gives an accurate account of the growth of the terminal plates, and shows that they form early in the career of the young Amphiura. He is doubtful whether they originate before or after the radialia, and regards it as probable that they are formed *before* the radialia or primary radials. Carpenter and Sladen § have discussed the homologies of the terminalia, adding no new facts, but drawing for illustration from the excellent paper of Ludwig so far as the development in this genus Amphiura is concerned. Sladen § says: "The primitive structure and mode of formation of the terminal plate is different from that of the first radial." It seems to me that the difference in primitive structure, if any, ought to have been more fully pointed out, and it is doubted whether there is any great difference in these particulars. I find nothing in Ludwig's account to justify the above statement of Sladen, and my own observations show that both the terminal plate and the first radial have many points of resemblance in "primitive structure" and "mode of formation." It is not intended to be denied that the form of the terminals and first radials may differ from the very first, or that they cannot be distinguished one from the other.

The terminals originate *after* the primary radials. This statement, hardly in accord with that of Ludwig, is supported by the figures of Krohn, Schultze, and Metschnikoff,† in which the terminals are much smaller than the radials, and in which the indications are that the latter are just forming. My own observations support the statement. I have never, however, recognized a young Amphiura with radials and without terminals. The terminal plate originates on the abactinal side of the water-tube, or "feeler," and by a growth of the arm is pushed out to the very end of the ray (Fig. 12). According to Lyman,|| the terminal plate is a hollow tube; and according to Ludwig,* it grows from the abactinal side around the feeler on both sides, joining on the actinal side. The

* *Op. cit.*, p. 187.

† *Op. cit.*, Pl. IV. Fig. 17.

‡ *Op. cit.*, pp. 187, 188.

§ *Op. cit.*, pp. 29, 30.

|| Ophiuridæ and Astrophytidæ, Old and New, *Bull. Mus. Comp. Zoöl.*, Vol. III. No. 10, p. 258, Pl. V. Figs. 1, 2, 3, 4.

end of the water-tube is said by him to pass through the tube thus formed.

The significance of the terminal plate has played an important part in discussions of Echinoderm morphology, and is by many thought to be the same as the ocular plate of the starfish. This opinion seems well supported; but whether the terminal or the radial is the homologue of the ocular of the sea-urchin is open to discussion.

As to the exact relationship of the terminal plate to other plates of the arm, it may be well to inquire whether it cannot be homologized with the so-called dorsal plate of the first or second adambulacral plates of the actinal region of the disk. That question will be considered, not answered, in our discussion of the dorsal plates of the arms.

When the arm is broken, a new terminal is formed by being pressed out by the growth of new plates, just as in the originally formed terminal plate. In the very instructive figures of the young of *Asterias glacialis*, Linn., by Lovén,* we have (Fig. 257) in the radial plate (*p*) a structure which may be considered the primary radial. If, however, we regard *p* as homologous to the radial plate, *rp*, of the Amphiura young, as its position on the radius would seem to indicate, its time of development, as compared with the interradials, *b*, is much retarded. It seems, indeed, not improbable that *p*, Fig. 257 (Lovén, *op. cit.*), is one of the series of plates along the middle aboral line of the ray, three of which are shown in Fig. 259. Possibly these plates are homologous with the dorsals of Amphiura and other Ophiurans. Lovén's figures (Figs. 256, 258) are interesting in another way. In the former of these, which is a view from the actinal side, in each interradius, there are two plates which in Fig. 258 bear spines. What are these plates? No one seems to have asked the question, as it is perhaps thought to be self-evident that they are adambulacral. As compared with the young Amphiura they have similarities with the second pair of adambulacral (ad^2). As in Amphiura these plates, although homologous to the lateral plates, are somewhat modified, so in the young *A. glacialis* they are somewhat different from other adambulacral plates. Among all the plates of the arm the terminal offers this peculiarity. It is the only plate which originates on the dorsal side of the water-tube and grows around it to the ventral. It therefore originates like a dorsal, and when grown occupies also the position of both laterals and possibly the ventral. Is it homo-

* Études sur les Échinoïdées, *Kongl. Svenska Vetenskaps Handlingar*, Bandet 11, No. 7. The plate *p*, according to Lovén, is a plate of the "système périsomatique." In the very young there is a single median series in this species.

logous to the other plates of the arms, and if so, to which, — dorsals or laterals or ventrals? In its mode of origin it is very much like a dorsal. It arises in the median dorsal line; it is single. It grows on the sides of the vessel as a lateral. With the ventral it has no resemblance. If it were possible to carry the homology of plates so far that every pair of adambulacral plates should have corresponding dorsals, it would be necessary to regard the primary radials as the dorsals of the first pair of radials, and then the terminals might be regarded as the dorsals of the second pair of adambulacrals. The third pair of adambulacrals would then be represented by true lateral plates, with a dorsal in the arm itself. This supposition and all similar theories seem to be overthrown by the fact that the terminal in the growth of the arm is pushed to its tip, far away from the plates with which it occupies relationships in early life. Whether it will be found that the terminal is a modified dorsal or lateral plate, or a plate unrepresented in other regions of the arm and disk, its fate in the formation of the arm is unique. While its early structure as a spicular calcification on the median radius resembles the radialia and the dorsal plates, its form in the adult is very different from these structures, and its relations to the water-vessel such as no other plate of disk or arms has.

Side Plates. — The side plates (*lp*) of the arms are regarded as adambulacral in their homology. They originate laterally and in pairs, growing dorsally and ventrally until they approximate dorsals and ventrals. The oldest side plates are adoral, and new side plates form between those already present and the terminals. The first pair of side plates originate *after* the *first ventral* (V), and before the arm has begun to push out. They therefore appear when first formed in the wall of the disk. Spines arise from the aboral edge of the side plates, those on the first pair of side plates being well formed before the fourth pair of side plates have appeared (Fig. 20). The time of the appearance of the side plates as compared with the first ventral will be seen, by a comparison of the above statement with that of Ludwig, to be contradictory. Ludwig says:* "Es entstehen aber die zu einem Armgliede gehörigen Seiten-Dorsal- und Ventralplatten nicht etwa auf einmal sondern zuerst sich nur die Seitenplatten an." While both V and V^1 (Pl. XI. Fig. 18, *op. cit.*) are regarded by him as ventral, especial attention is turned by Ludwig to V^1 as the first ventral, in his reference to the sequence of the formation of the side plates and ventrals. I believe that the contradiction pointed out between Ludwig's account of the sequence of these plates and my own is apparent

* *Op. cit.*, pp. 188, 189.

rather than real; for the ventral plate *V* belongs to the first pair of adambulacral plates (ad^1), which are themselves homologous with side plates. Although the first ventral (*V*) is formed before the first side plates, it appears after the first adambulacral pair to which it belongs. Considering these facts, the law pointed out by Ludwig,* that the side plates precede the ventral in time of formation, holds likewise for the first adambulacral, and is true of the side plates if we give them their true interpretation as adambulacral plates.

Ventral Plates. — The ventral arm-plate or under arm-plate is early developed in the young Amphiura. The first ventral (*V*) is already well formed when the terminal plate has just begun to push its way axially from the periphery of the disk. The first ventral plate (Figs. 16, 17) is formed before the first side plates of the arm, but after the first adambulacral. Ludwig * states: "Erst nachdem die Seitenplatten sich angelegt haben, beginnen auch die Dorsal- und Ventralplatten aufzutreten und zwar sind wenigstens bei *Amphiura squamata* die Ventralplatten den Dorsalplatten immer ein wenig voraus." I have already spoken of this sequence in my account of the side plates. It is here for the first time suggested that the plate *Vv* is the ventral plate of the first or second pair of adambulacrals. If it (*V*) is a ventral plate of the true side plates, it is more rapid in its growth, as compared with the true side plates, than the other and subsequently formed ventrals.

The ventrals *originate on the median ventral line, and are unpaired.* They first appear as a trifid spicule (Fig. 20, *v*), one prong of which is adoral, the others aboral and lateral. In early formation they are free, and do not arise from the lateral arm-plates. They precede, in time of formation, the corresponding dorsal of the same joint; and while in most particulars the growth of the new plates resembles the growth of those of a repaired arm of an Ophiuran as described by Lyman,† the sequence of dorsals and ventrals does not seem to agree with the descriptions by the last-mentioned author, who says that in a repaired arm the upper (dorsal) plate is first formed.

Ventrals never arise by coalescence of plates on either side of the middle line of the arm.

* *Op. cit.*, p. 189.

† Ophiuridæ and Astrophytidæ, Old and New, *Bull. Mus. Comp. Zoöl.*, p. 258. "Then appear on the central point of juncture, above, clusters of grains which in time grow into upper arm-plates, and a similar process follows for the lower arm-plates." The fact that the dorsal arm-plate in Amphiura originates as a single spicule after the ventral has a meaning as compared with certain embryonic genera. (See p. 145.)

In a discussion of the relationship of the genus Brisinga to the Ophiurans, A. Agassiz * has sought to show that it is an intermediate genus, connecting starfishes and Ophiurans. He finds the homologues of the ventral plates of the Ophiuran in the fusion of the interambulacral plates along the median line of the arm. He says: "In the case of the Ophiurans . . . the lower arm-plate is formed by the junction of opposing spurs of the interambulacral plates, as can readily be imagined from a comparison with Brisinga, where we find a spur from the interambulacral plates extending nearly two thirds across the arms." That there are anatomical, perhaps embryological, grounds upon which Brisinga may be regarded as reducing the "gap hitherto unfilled between starfishes and Ophiurans," is not doubted; but it may well be questioned whether the ventral plate of Amphiura, originating as it does on the median line and later than the corresponding lateral plates, is homologous to any part of the interambulacral plates of Brisinga.

A. Agassiz † states that "a row of limestone cells extending along the median line separates the base of the suckers," and that the embryo starfish has no trace of any interambulacral system. He calls attention (p. 53) to the absence of a well-defined interambulacral system of plates in a young starfish (Pl. VIII. Fig. 9), in which the rays are well developed, and considers the young starfish as still eminently Ophiuroid in most important embryonic features. He shows a distinct row of "median ambulacral spines (u^1)" on the abactinal side of the arms. These plates with spines are those supposed from A. Agassiz's description to be formed as follows: The radial plates of the abactinal system of the "dorsal part of the arms gradually extend towards the edge of and down on to the actinal side, enclosing the water-system little by little, and finally, as has been described, covering the ambulacral tube," etc. The median plates are later, according to A. Agassiz, ‡ absorbed along the median line in Asteracanthion. It would appear then that from the unabsorbed end of these plates, homologous with the adambulacral plates, grow the ambulacral plates above, or on the abactinal side of the water-system into the position which they eventually have in the adult. In the Ophiurans the median plate of the starfish before absorption of the plate is represented, according to him, by the lower arm-plates (ventrals). The Ophiurans are regarded as remaining in an embryonic condition so far as these plates are concerned.

Aside from the fact already commented upon, that in Amphiura the

* *Mem. Mus. Comp. Zoöl.*, Vol. VI. p. 102.

† Embryology of Starfish, p. 47.

‡ *Op. cit.*, p. 92.

ventral plate is a median actinal deposit, and not, as in the starfish, joined by the growth of plates to the median line to form the embryonic median plate, the author finds this difficulty in the homology indicated above. It would seem from the description that both ambulacral and adambulacral were derived from the same calcification in Asteracanthion, a calcification beginning on the abactinal and growing down on each side to the actinal median coalescence. In Amphiura ambulacral and adambulacral plates are from the first separate and distinct calcifications.

In the abbreviated development of Asterina as given by Ludwig there seems to be a wide difference in the growth of the plates from that of Asteracanthion recorded by A. Agassiz. Adambulacral and ambulacral plates are recorded by the former from the very first, and in the oldest stage figured no embryonic median actinal row of spiniferous plates is figured in the arm. *Asterias glacialis* seems also, according to Lovén's figures, to differ from Asteracanthion in this particular. The plates which appear to correspond with the lateral ambulacra of A. Agassiz's account seem to be separated along the median line of the arm on the actinal side, and median plates below the water-vessel or its position are not figured. Perhaps no genus of starfishes can better serve to explain these discrepancies than Pteraster. The embryology of this starfish is very much needed, and from the interesting fact that the young is carried in a pouch on the abactinal surface of the body, and is therefore probably without a brachiolaria, we may expect interesting revelations from its study.

If one cannot accept the theory that the ventrals of Amphiura are homologous with the embryonic median plates of the young starfish, Asteracanthion, and cannot regard them as formed from the adambulacral plates by coalescence along the median line, it may be asked, What are they, and to what plates in the starfish are they homologous? In answer to this question we might ask another, Why is it necessary to suppose that they are represented in the starfish? We know that there are plates on the dorsal hemisome of Amphiura which seem not to be represented in the starfish. Why not suppose that the ventrals are unrepresented? Perhaps they belong neither to ambulacral nor interambulacral systems, but are special plates for the protection of the nerve and water system of the arms. Perhaps also similar coverings of the Echinoid are also not referable to either ambulacral * or interambulacral systems, as we under-

* Ludwig regards the ambulacral plates of the starfish as unrepresented in the sea-urchin, or highly modified into the auricles. This homology of what are commonly called the ambulacrals in the sea-urchin with the adambulacral of starfishes

stand it, but to special plates not represented in the starfishes, Asteracanthion, or Asterina, young or old.

Dorsal Plates. — The dorsal or upper plates of the arm (Fig. 19, *d*) originate in the median dorsal line as simple trifid spicules, and form in series from the adoral to the terminal, the adoral being the oldest. The last formed is nearest the terminal. In their first condition they resemble the ventrals, and the subsequent growth is similar. The dorsal appears after the corresponding ventral. This fact is an interesting one in comparative anatomy. Many genera of Ophiuridæ (Ophiohelus, Ophiambyx, and others from deep seas) and all the Astrophytidæ are destitute of dorsals. In these Ophiuridæ the ventrals are present, and in the Astrophytidæ the first ventral is developed while others are wanting. The dorsals disappear before the ventrals, if the want of dorsals in these low genera is due to degradation, or the genera have not progressed through embryonic stages in which dorsals appear, if, as is probably the case, dorsals have never appeared. In the growth of Amphiura the ventrals form first, and those genera with a single ventral and no dorsal may be compared with my Fig. 17, Pl. III.

I am led to suppose that the dorsals have been inadvertently omitted in certain of the figures of a young Amphiura by Ludwig (Pl. XI. Figs. 21, 25), for he has not represented these plates in a young specimen in which three pairs of side arm-plates are represented (Pl. XI. Fig. 21, ad^3, ad^4, ad^5). In a young Amphiura of about the same age (Pl. III. Fig. 19) at least one dorsal plate is formed, and in another as old as that represented in his Fig. 25 (same plate) the dorsals have increased in number. In none of Ludwig's figures are dorsals represented, although in Figs. 21, 25, they must have been already formed.

The dorsal originates adaxially to its side plates on the median line, as shown in my figures.

would explain the position of the water-vessel in the former group. We must look with interest to the method of growth of these plates in sea-urchins much younger than any yet studied for a solution of this question.

As the viviparous Amphiura and the Asterina with the direct development have thus far furnished the best information in regard to the method of formation of the plates in Ophiurans and starfishes, perhaps the growth of the plates in Echinoids can best be revealed by the life history of the Hemiaster of the South Sea, with young in pouches in the ambulacral zones. Although the young Hemiaster has been well described by A. Agassiz, Thomson, and others, the growth of the young plates is as yet not well enough known for comparison.

The following summary may be made of the preceding observations: —

1. The intestine of the bisymmetrical larva is early developed, and later in development becomes atrophied and is lost.

2. The mouth and œsophagus (?) of the bilateral larva is formed by an invagination of the epiblast while yet the larva is enclosed in its sac and attached to the parent.

3. The provisional skeleton of the bilateral larva is not always symmetrical, and sometimes develops on one side. The first-formed rod is not always a trifid calcification.

4. An umbilical connection exists in all later stages of growth until the pentagonal form is assumed. The relation of the umbilicus to the mouth, stomach, and intestine is described.

5. The first calcareous plates to form on the abactinal hemisome are five first radials, and a little later a dorsocentral. The radials antedate the terminals.

6. The first plates to form on the actinal hemisome are the first adambulacral.

7. The second pair of adambulacral plates bear club-shaped spines. These last structures are homologous to the spines of the lateral plates of the arms.

8. The first ventral plate to form belongs to the first pair of adambulacral plates, and not to side plates of the arms. This first ventral, although not belonging to the portion of the arm free from the disk, is homologous to the other ventral arm-plates.

9. The radial shields originate before a plate called the "underbasal" forms between the dorsocentral and the primary radials, and while there are but two intermediate plates in each of the interradii.

10. The homology of certain plates of the young Amphiura to the basals, as suggested by Carpenter, is discussed, and doubts advanced whether the individual plates mentioned by him are basals in preference to other interradial plates.

11. The ambulacral plates do not always originate as trifid spicules, but sometimes first appear as parallel unbranched rods.

12. *A. squamata* is infested by a parasitic Crustacean, which, although in adult form closely allied to a Copepod, lays eggs in packets in the host. These ova were found in conditions of cleavage, in a nauplius stage and in intermediate conditions. The adult is also found in the Amphiura. Eggs *not* attached to adult.

The following summary may be made of new figures, or new anatomical details first figured : —

1. Figures (Pl. I. Figs. 1, 2) of plutei of Ophiopholis older than that figured in *Bull. Mus. Comp. Zoöl.*, XI. 4, Fig. 23, and younger than adult. Figure (Pl. I. Fig. 3) of an adult pluteus of Ophiopholis.

2. Figures (Pl. II. Figs. 5, 7, 8) of the umbilical connection of the bilaterally symmetrical young with its parent. These differ from those of Max Schultze in showing the relation of this structure to internal organs. In Apostolides' and Metschnikoff's figures of the bisymmetrical larva this structure is not represented. Figure (Pl. II. Fig. 4) of a larva with a single asymmetrical pluteus spine. Figures (Pl. II. Figs. 13, 14) of the actinal and abactinal hemisome of a young Amphiura of an age between that figured by Ludwig on Pl. XI. Figs. 17, 23, and Pl. XI. Fig. 19.

3. Figure (Pl. III. Fig. 20) of the actinal hemisome of a young Amphiura older than Ludwig's Pl. XI. Fig. 18. This figure shows structures purposely omitted in all Ludwig's figures, viz. spines and club-shaped bodies, appendages of the second pair of adambulacral. Figure (Pl. III. Fig. 17) older than Ludwig's Pl. XI. Fig. 19 and younger than his Pl. XI. Fig. 18, illustrating the formation of the first side plates of the arms. Figure (Pl. III. Fig. 19) illustrating the relative situation of the dorsals. Dorsals are omitted in all Ludwig's figures of the arm from the abactinal side. My figure is younger than his Pl. XI. Fig. 21, in which a dorsal ought to be represented. Figure (Pl. III. Fig. 15) showing the arm-joints or ambulacral plates of the arms *in situ* and before coalescence.

CAMBRIDGE, January, 1887.

EXPLANATION OF THE PLATES.

LETTERING.

a.	Opening into the supposed cavity of the blastosphere, blastopore ?
*ad*¹.	First pair of adambulacral plates.
*ad*².	Second pair of adambulacral plates.
al.	Anal lobe.
alr.	Anterolateral rod.
ar.	Anterior rod.
c.	Infolded epiblast.
cav.	Cavity, segmentation cavity.
cr.	Calcareous trifid spicules.
d.	Dorsal plate, upper arm-plate.
dc.	Dorsocentral plate.
eb.	Epiblast.
f.	Feeler, leg, paired feeler.
ga.	Stomach.
i.	Intestine.
ir.	Interradial plate.
lp.	Lateral arm-plates, adambulacral, side-plates.
lr.	Lateral rod.
ls.	Lateral "Scheibe," enterocœl on left side.
lw.	Left-water tube or hydrocœl.
m.	Madreporic opening.
*m*¹.	Inner layer or envelope of the segmentation spheres.
*m*².	Outer layer or envelope.
mb.	Mesoblast.
mbc.	Mesoblastic cells } "Mesenchyme ?"
o.	Oral plate.
os.	Ambulacral plates, "ossicles," "arm bones."
oe.	Œsophagus.
or.	Mouth.
pig.	Pigment.
pr.	Posterior rod.
ps.	Pluteus spine.
rp.	Radial plate, first radial.
*rp*². } *rp*³. }	Plates of disk formed after the first radials.
rs.	Radial shield.

rw. Right water-vessel, hydrocœl.
sp. Spine of arm.
spl. Spoon-shaped plate.
t. Teeth.
tf. Unpaired or terminal feeler. See *wt.*
to. Torus angularis, jaw-plate.
tp. Terminal plate, terminal.
u. Connection of pentagonal larva with parent. In stages earlier than pentagonal larva also found.
v. Ventral plate, lower arm-plate.
wt. Terminal end of water-vessel of the arm.

PLATE I.

Figures drawn with Camera lucida, Obj. BB.

Fig. 1. Pluteus of *Ophiopholis aculeata*, Gray, in a little older condition than that figured in Fig. 23, Pl. I., *Bull. Mus. Comp. Zoöl.*, Vol. XII. No. 4.
" 2. The same somewhat older. Seen from side on which mouth opens.
" 3. Adult pluteus of *O. aculeata* before young Ophiuran has begun to form.

The drawings from which these figures were made are from plutei taken at Frye's Island, New Brunswick. This island bears the name of Cailiff's Island on the Admiralty Chart.

The same plutei are common at Eastport, Maine.

PLATE II.

Figures drawn with Camera, Objs. BB, DD, Zeiss. All except Fig. 1 *with Obj. BB.*

Fig. 1. Blastosphere of *Amphiura squamata*. Diameter, .15 mm.
" 2. Same, younger.
" 3. Gastrula.
" 4. Ventral view of a bisymmetrical larva, unattached.
" 5. The same, lateral view, attached.
" 6. Somewhat older larva than the last, showing the vasoperitoneal sacs or water-tubes.
" 7. The last, lateral view, unattached. The remnant of the attachment in the upper right-hand corner.
" 8. An older larva than the last, attached. Dorsal view.
" 9. The same, older.
" 10. The same, still older.
" 11. Somewhat older larva.
" 12. A pentagonal attached larva with well-formed radial, dorsocentral, and terminal plates. Abactinal view. Attachment at *u.*
" 13. Youngest free Amphiura, unattached to parent. Found free in mother. Abactinal view. The great prominence of two of the terminal plates, *tp*, is due to the position which the specimen had when drawn.

Fig. 14. An older larva from the body of parent. Abactinal view. The club-shaped bodies ad^2 are spines of the second pair of adambulacrals, which in this stage project beyond the periphery of the disk.

PLATE III.

Fig. 15. View of the calcareous plates of the actinal side of the disk of Amphiura in a pentagonal larva younger than Pl. II. Fig. 13.

" 16. One fifth of the actinal hemisome of an older pentagonal larva than last. This figure has, in addition to plates of Fig. 15, the ventrals *v*, and orals *o*.

" 17. Pentagonal larva, actinal view, older than last, showing the origin of the lateral plates *lp*.

" 18. Abactinal view of an older larva in which the arms have increased in length, the terminal plate being pushed outward by the formation of the lateral and ventral plates. One arm is shaded, two adjacent arms drawn in outline, and two arms not represented.

" 19. The arm and portion of the abactinal hemisome of an older Amphiura. Three pairs of lateral arm-plates are represented, and two dorsals are shown. Abactinal view.

" 20. An arm and portion of the actinal hemisome of a larva about the same age or slightly older than the last.